

Diet, Feeding Habits and Estimates of Daily Ration of Young Lemon Sharks, *Negaprion brevirostris* (Poey)

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The diet of a tropical elasmobranch, the lemon shark, *Negaprion brevirostris*, was investigated through analyses of stomach contents collected during two sampling periods. Data set 1 consisted of the stomach contents of 78 young and sub-adult specimens caught in the Florida Keys and at Bimini, Bahamas, from 1981-85. Data set 2 ($n = 86$) consisted of newborn and young specimens only, captured in the Florida Keys during the summer of 1986. In the two data sets teleosts were the dominant prey, followed by crustaceans and mollusks. Stomach contents from data set 2 were used to study food consumption parameters and estimate daily ration. About a quarter of the stomachs in each data set were empty. No pattern in diel feeding activity or differences in the amount of food consumed by males or females were found. Feeding in the population was asynchronous and intermittent, with a maximum duration in 11 h. Five methods were applied to determine daily ration. Three of these methods were based upon collection of data on stomach contents of sharks caught in the wild. The other two were laboratory-based approaches. Estimates of daily ration ranged from 1.5-2.1% of the shark's body weight.

TO understand the trophic dynamics of a marine ecosystem one must evaluate the influence of top predators. Food habit and food consumption studies are useful tools in such an evaluation. Because studies dealing with sharks

are few, knowledge of the role of this important group of "apex" predators in the sea, and especially in the tropics is still very rudimentary (Gruber, 1982).

The lemon shark, *Negaprion brevirostris*, is a

coastal, tropical shark, abundant in the shallow waters of south Florida and the Caribbean, which serve as nursery grounds for this species. Newborn and young lemon sharks commonly occur at mangrove fringes and on shallow grass beds in enclosed sounds or bays throughout the Florida Keys. Yet knowledge of the diet and feeding habits of this shark is still fragmentary. Qualitative attempts have been made to describe its diet (Springer, 1950; Clark and von Schmidt, 1965; Dahlberg and Heard, 1969), and quantitative information on the diet of 18 young lemon sharks was provided by Schmidt (1986). However, no studies have dealt with the daily food intake of the lemon shark and only a few such studies have been conducted on other species of sharks (Medved et al., 1988; Jones and Geen, 1977; Stillwell and Kohler, 1982).

The purpose of the present paper is to: 1) analyze quantitatively the diet of lemon sharks in the Florida Keys and Bimini, Bahamas; and 2) gain some insight into the food habits and estimate the daily ration of young lemon sharks in the Florida Keys. We will show that the lemon shark appears to be an opportunistic piscivore, with no apparent pattern of diel feeding, that consumes about 2% of its body weight (BW) daily.

MATERIALS AND METHODS

Source and handling of sharks.—Stomach contents of lemon sharks were collected during two sampling periods. Data set 1 consisted of stomach contents from 78 lemon sharks (34 males, 40 females, four sex not determined), ranging in precaudal length (PCL) from 47–205 cm. These sharks were captured in gill nets and by hook and line in the Florida Keys, near Lower Matecumbe Key and Marathon (58 animals), and in Bimini, Bahamas (20), during 1981–85. Choice of the collection sites for data set 1 was based solely on convenience and availability of specimens. It was not the purpose of the present study to compare the diet of the sharks from the Florida Keys and from Bimini, Bahamas. Data set 2 consisted of stomach contents from newborn and young lemon sharks, which were also used to study feeding habits and estimate daily ration. For this reason, samples were obtained at hourly intervals. All sharks in data set 2 were collected at mangrove fringes and on shallow grass flats in several areas of the Florida Keys. This set consisted of 64 stomach contents

from 86 sharks (43 males, 43 females), ranging from 43–83.7 cm PCL ($\bar{x} = 58.1 \pm 8.4$ SD) and from 0.821–7.086 kg in weight ($\bar{x} = 2.417 \pm 1.18$ SD), caught at Lower Matecumbe Key (17 animals), Marathon Key (8), and Big Pine Key (61) during July and Aug. 1986. To avoid the bias of attraction by bait, which resulted in up to 80% of animals with empty stomachs in earlier studies (Gruber, 1984), these sharks were captured in monofilament gill nets. Four sections of gill net were used: two were 91 m long, 1.8 m deep, with 15 cm stretched mesh; and two were 91 m long, 1.2 m deep, with 12.5 cm stretched mesh. The nets were set in waters ranging from 15–120 cm and the float line was continuously observed from a nearby boat. The sharks were immediately removed from the net and then weighed, measured, sexed, identified as to time and place of capture, and marked by punching holes in the fins. Each shark was then anaesthetized lightly by placing it in a foam-lined box containing approx. 15 liters of water and 1.5 g of tricaine (MS 222). When the shark was immobilized, the stomach was everted by positioning the shark vertically, snout down, over a collecting tray, and by using forceps to reach into the shark's stomach. The recovered contents were stored in plastic containers filled with 250 ml of 70% isopropanol. After this stomach eversion, the shark was force-fed a piece of snapper (*Lutjanidae*) or grunt (*Haemulidae*) and a multivitamin tablet, and was released safely away from the net.

Laboratory and data analysis.—Identification of stomach contents was carried to the lowest possible taxonomic level. For each food item, excess water was removed by blotting it on filter paper. The volume of each food item was then determined by water displacement to the nearest ml in a graduated cylinder, and wet weight was determined by weighing on an electronic balance to the nearest 0.1 g. In addition, for data set 2, the total length of each food item was taken when possible and an arbitrary stage-of-digestion value from 1–7 assigned (Table 1). The digestion values were based on prior observations of fishes in various stages of digestion, made during a field study of gastric evacuation (Cortés, 1987) in which young lemon sharks kept in an enclosure in the natural environment, at temperatures ranging from 21–27°C, were fed preweighed meals of snapper, *Lutjanus* spp., or white grunt, *Haemulon plumieri*. The stomach contents were recovered at

TABLE 1. QUALITATIVE STAGE-OF-DIGESTION SCALE FOR SNAPPER AND WHITE GRUNT FED TO YOUNG LEMON SHARKS, *Negaprion brevirostris*, AT A MEAN TEMPERATURE OF 25 C. The description of remains includes only headless fish; each value from 1-7 is equivalent to a time span of approx. 5 h.

Stage of digestion value	Time after feeding (h)	Description of remains
1	5	Almost intact; some scales detached.
2	10	More scales detached; some flesh loss, but backbone still intact with flesh and most of scales attached.
3	15	Some scales still attached; backbone first exposed; more flesh loss.
4	20	Backbone more visible; flesh still attached; most of scales detached.
5	25	Backbone visible and centra separating; some flesh still attached.
6	30	Pieces of backbone and spines; hardly any flesh left.
7	35	Some scales, part of backbone, spines in fluid matrix; no flesh left.

varying time intervals after feeding (approx. every 3 h) by using the stomach-eversion technique described above. These values were used as standards to estimate the time of consumption for prey items taken from the stomachs of sharks in data set 2. The duration of feeding activity for each shark was assessed by comparing the difference between stage-of-digestion values for the first and last ingested item in each stomach (Diana, 1979). Each food item was then dried in an oven at 60 C for 72 h and placed in a vacuum desiccator for an additional 24 h until constant weight (dry weight) was achieved. Samples for the most representative food items were ground in a Willey mill (General Electric), and 0.1 g pellets were made from the powder. Subsamples were either combusted completely in an adiabatic bomb calorimeter (Parr, Inc.) to determine energy content, or burned in a muffle furnace at 600 C for 24 h to determine ash content. Data for the species for which calorimetry was not performed were obtained from other sources (Thayer et al., 1973; M. Cummings, pers. comm.). The mean energy value of food consumed was the sum of the energy

value of each individual species multiplied by the percentage contribution of that species to the diet.

Stomach capacity was measured for 23 young lemon sharks in the size range of the specimens in data set 2 (i.e., 45.5-83.7 cm PCL). It was done by removing the stomach, ligating the pyloric valve, and completely filling the stomach with water from a graduated cylinder. However, we realize that this approach provides only a rough estimate of actual capacity, since the stomach can probably become more distended in a live animal.

The contribution of different prey items to the shark's diet was determined by the following quantitative methods (Pinkas et al., 1971; Hyslop, 1980): 1) numerical importance (%N), the number of items in each prey category, expressed as a percentage of the total number of prey items; 2) frequency of occurrence (%F), the ratio of stomachs containing a particular prey compared to the total number of stomachs containing prey and expressed as a percentage (the sum of the values will exceed 100% because several prey types can be found simultaneously in a single stomach); 3) gravimetric importance (%W), the wet weight of a prey category compared to the total weight of the stomach contents, expressed as a percentage; 4) relative importance index (RI), based on the "absolute importance index" (AI), which is calculated as $AI = \%F + \%N + \%W$ and

$$RI = 100 \frac{AI}{\sum_{i=1}^n AI_i}$$

where n is the number of different food types.

The weights of stomach contents were not normally distributed but instead were highly skewed towards the lower weight values. Therefore, to test hypotheses concerning the weights of stomach contents (e.g., as to whether males fed more heavily than females), the data were either log-transformed to render them normal or non-parametric techniques applied (Sokal and Rohlf, 1981).

Methods of estimating daily ration.—We applied five methods to estimate daily ration. Three of these methods were based upon collection of stomach contents of fish sampled in the wild and require prior knowledge of the rate of digestion. We urge the reader to refer to the original articles for more details on each of these methods:

1) Elliott and Persson method (1978): this

model assumes that feeding is continuous and constant, and food consumption (C_t) between time t_0 and t_1 is given by:

$$C_t = (S_t - S_0 e^{-Rt}) / (1 - e^{-Rt}) \quad (1)$$

where S_0 and S_t is the amount of food in the stomach at time 0 and t respectively, t is time interval between samples, and R is the instantaneous rate of gastric evacuation.

For this method a sample of fish is collected from the field at intervals of t hours during a 24 h period, and the mean weight of stomach contents is used to estimate S_0 and S_t for each time interval. To obtain the daily ration, the estimates at each time interval are summed over 24 h. Elliott and Persson (1978) indicated that even if feeding is not continuous, their model will produce an unbiased estimate of actual food intake if t is kept to 3 h or less.

We used a value of $R = -0.175$, determined by Schurdk and Gruber (1989) in a controlled experiment in which captive lemon sharks were fed a 2.7% body weight (BW) meal of a carangid fish, the blue runner, *Caranx chrysos*, at 25°C.

2) Diana method (1979): this model was developed for a top carnivore, the northern pike, *Esox lucius*, and assumes that gastric evacuation is an exponential process, feeding is asynchronous and intermittent, and feeding rates are short while the interval between meals is longer than digestion time. This model uses the stomach contents of fish collected in the wild to determine feeding frequency and establish meal size and meal ingestion times. Meal frequency (F) can be estimated by the expression:

$$F = B / 1 - E \quad (2)$$

where B is total time to complete gastric evacuation, and E is the proportion of empty stomachs in the population.

To estimate meal size, a qualitative scale for evaluating the degree of digestion of an item is established for each food item. The qualitative stage-of-digestion scale we used was based on only two prey items (Table 1). This scale permits an estimate of time elapsed since feeding (t). By substituting this time into the appropriate gastric evacuation expression and knowing the instantaneous rate of gastric evacuation (R), the percentage of food remaining in the stomach (S_t) can be estimated. This value can then be applied to the measured weight of food in the stomach to back-calculate meal size (S_0). Once meal frequency (F) and meal size (S_0) are estab-

lished, daily ration can then be calculated as S_0/F .

Based on the work of Schurdk and Gruber (1989) and Cortés (1987), two different equations were used to determine the percentage of food remaining in the stomach. Schurdk and Gruber found that blue runner filets were completely evacuated from the stomach of young lemon sharks in approx. 24.5 h, and that the pattern of emptying was exponential. Cortés (1987) found that a meal of natural prey items, such as snappers or white grunts, was evacuated in 28–41 h, and that the pattern of evacuation was best described by a linear model. The difference in the evacuation times and models between these two studies may be explained by the use of smaller more friable food by Schurdk and Gruber. Jobling (1987) reviewed the effect of the type of food on gastric evacuation in fish and concluded that smaller more easily digested food is eliminated from the stomach in an exponential manner, while larger items are evacuated in a linear manner. Thus, the equation:

$$S_t = S_0 e^{-Rt} \quad (3)$$

where $R = -0.175$ (Schurdk and Gruber) was used to describe gastric emptying and reconstruct meal size of small, easily digestible prey items, whereas:

$$S_t = S_0 - Rt \quad (4)$$

where $R = -3.002$ (Cortés, 1987) was used for larger food items, assumed to be more difficult to digest.

3) Olson and Mullen method (1986): this model was also developed for a predator, the yellowfin tuna, *Thunnus albacares*, and assumes that the predator eats a variety of prey which are evacuated at different rates. However, it does not require the rate of gastric evacuation to be exponential. The absolute quantity of food (W) remaining from any single meal (M) is expressed as:

$$W = Mf(t) \quad (5)$$

where $f(t)$ is the known proportion of food remaining in the stomach t time units after a single meal. If \bar{W} is the product of several meals taken at several intervals, the following expression is finally obtained:

$$\bar{W} = (\bar{M}/\bar{T}) \int_0^\infty f(t) dt \quad (6)$$

where \bar{M} is mean meal size and \bar{T} is mean in-

interval between meals, $r = \bar{M}/\bar{T}$ is the feeding rate, and if A is defined as the integral of the function fit to gastric evacuation data:

$$A = \int_0^{\infty} f(t) dt \quad (7)$$

then $r = \bar{W}/A$. \bar{W} can be estimated by weighing the stomach contents of fish sampled at random times, or if it can be assumed that the fish feed at random intervals; $f(t)$ is given by gastric evacuation experiments. If we assume meals are mixed (i.e., a variety of prey types are consumed), and evacuated at different rates, then:

$$r = \sum_{i=0}^I \bar{W}_i/A_i \quad (8)$$

where i refers to each of the I prey types. For this model we derived a feeding rate (r) for each of the two prey categories also considered for the Diana model, such that equation (8) becomes:

$$r = \sum_{i=0}^I \bar{W}_i/A_i = \bar{W}_{exp}/A_{exp} + \bar{W}_{lin}/A_{lin} \quad (9)$$

where \bar{W}_{exp} and \bar{W}_{lin} are the mean weights of the food items digested in an exponential and linear way respectively, and A_{exp} and A_{lin} are the proportions of the food items remaining in the stomach which have been digested in an exponential and linear way respectively. For the small, friable prey:

$$r = \bar{W}/\int_0^{\infty} e^{-Rt} dt = \bar{W}R \quad (10)$$

which is the Elliott and Persson equation to estimate daily food consumption (Mullen, 1986), where $R (= -0.175)$ is the constant exponential rate of gastric emptying.

For the larger food items:

$$r = \bar{W}/\int_0^{1/R} (1 - Rt) dt = \bar{W}2R \quad (11)$$

where $R (= -3.002)$ is the linear rate of gastric evacuation expressed as a percentage by hour (%/h). Daily meal is then calculated by multiplying r by 24, and daily ration is daily meal expressed as a percentage of the mean wet body weight of the sharks composing the data set (2420 g).

4-5) Laboratory methods: the two other methods we applied to estimate daily ration were

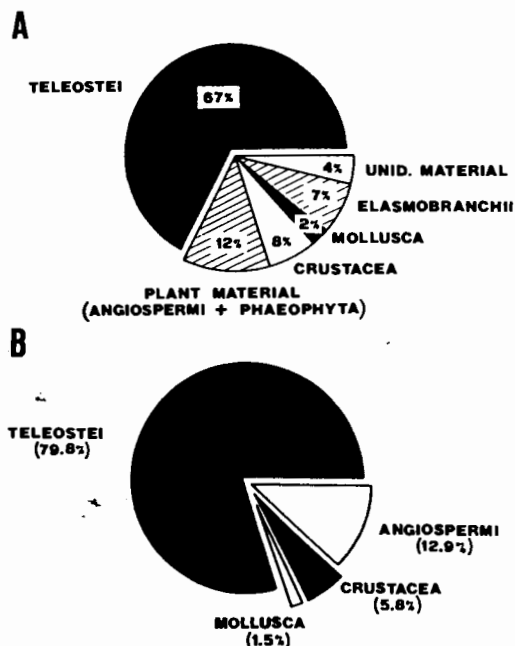


Fig. 1. Major food categories in the diet of the lemon shark, *Negaprion brevirostris*, expressed by the RI. RI is calculated for each food type as the sum of the frequency of occurrence (%F), the percentage by number (%N) and the percentage by weight (%W) expressed as a percentage of the total %F, %N and %W for all food types: A) data set 1 ($n = 78$); B) data set 2 ($n = 64$, young sharks only).

laboratory approaches. In one of these methods (see L-1 of Table 5), a ration-production relation is derived in the laboratory, and daily ration in the wild is estimated as the food intake level that would provide for the growth of the fish observed in nature, which is in turn obtained from weight-length relations and mark-recapture data. Growth of free-ranging animals was obtained from Henningsen and Gruber (unpubl.). For a standard age-0, 1309 g lemon shark, growth in its first year of life is 130 mm/yr, equivalent to 1388 g or an average 3.8 g/d of new fresh tissue for an average 0.5 yr old 1931 g shark. This value was then plotted in the ration-production relation derived in the laboratory by Cortés (1987) and a value of daily ration back-calculated.

In the other laboratory method (see L-2 of Table 5) one estimates growth, metabolism, and excretion and substitutes them in the energy equation (Winberg, 1960):

$$C = 1.25(G + M) \quad (12)$$

TABLE 2. SUMMARY OF FOOD CATEGORIES IN THE DIET OF 78 YOUNG LEMON SHARKS, *Negaprion brevirostris*, FROM THE FLORIDA KEYS AND BIMINI, BAHAMAS (DATA SET 1), EXPRESSED AS PERCENT BY NUMBER (%N), FREQUENCY OF OCCURRENCE (%F), AND PERCENT WEIGHT (%W). Also shown is the RI, which is calculated for each food type as the sum of %N, %F and %W, expressed as percentage of the total %N, %F and %W for all food types.

Food item	%N		%F		%W		RI
	n	%	F	%	wt (g)	%	
Pisces	115	69.3	93	119.2	1763.0	93.6	73.6
Teleostei	110	66.3	88	112.8	1432.0	76.0	66.6
Ariidae	2	1.2	2	2.6	24.5	1.3	1.3
Atherinidae	8	4.8	2	2.6	6.0	0.3	2.0
Batrachoididae	7	4.2	5	6.4	65.0	3.5	3.7
Blenniidae	6	3.6	3	3.9	17.0	0.9	2.2
Carangidae	6	3.6	5	6.4	128.5	6.8	4.4
Centropomidae	1	0.6	1	1.3	83.5	4.4	1.6
Elopidae	1	0.6	1	1.3	46.5	2.5	1.1
Gerreidae	1	0.6	1	1.3	65.0	3.4	1.4
Hemiramphidae	8	4.8	7	9.0	60.0	3.2	4.4
Lutjanidae	9	5.4	8	10.2	260.5	13.8	7.7
Monacanthidae	2	1.2	2	2.6	20.0	1.1	1.3
Mugilidae	2	1.2	2	2.6	7.0	0.4	1.1
Ophichthidae	7	4.2	5	6.4	80.0	4.2	3.9
Unid. eels	4	2.4	3	3.8	1.5	0.1	1.6
Ostraciidae	2	1.2	2	2.6	18.5	1.0	1.2
Soleidae	3	1.8	2	2.6	8.0	4.0	1.2
Sparidae	9	5.4	8	10.2	140.0	7.4	6.0
Tetraodontidae	1	0.6	1	1.3	4.5	0.2	0.6
Unid. teleosts	31	18.7	28	35.9	395.5	21.0	19.7
Elasmobranchii	5	3.0	5	6.4	331.0	17.6	7.0
Mollusca	5	3.0	4	5.1	0.1	0.01	2.1
Crustacea	14	8.4	14	17.9	68.5	3.6	7.8
Angiospermi	23	13.8	23	29.5	7.0	4.0	11.4
Phaeophyta	2	1.2	2	2.6	1.5	0.1	1.0
Unid. material	7	4.2	7	9.0	42.5	2.3	4.0

where C is the energy value of the food consumed, 1.25 is a correction factor for non-assimilated food, G is the energy for growth, and M is the total energy of metabolism. We used the estimate of field growth for age-0 lemon sharks (3.8 g/d) and converted it into joules by using a fresh weight energy value of 5.41 kJ/g determined by Cortés (1987). For the other unknown, M, we used the average daily metabolic rate of 67.8 kJ·kg⁻¹·d⁻¹ at 25°C, based on an oxy-caloric value of 20.9 J/ml O₂ (Bushnell, 1982). Metabolic rate was then corrected for the average weight of the fish in the sample (2420 g). The values of G and M were then substituted in the energy budget equation. Using the energy value of food consumed, the daily ration may be obtained. We used an energy value for the food consumed of 5.05 kJ/g wet

weight (average of 4.6 kJ/g for food consumed in the field and 5.5 kJ/g for food consumed in the laboratory; Cortés, 1987).

RESULTS

Diet.—Data set 1: Of the 78 stomachs examined, teleost fishes were the major food category on a per number (66.3%), frequency (112.8%), and wet weight basis (76%). Crustaceans, elasmobranchs, and mollusks were less common (Table 2). The RI showed that teleosts comprised 67% of the diet, whereas crustaceans, elasmobranchs, and mollusks comprised 8%, 7%, and 2%, respectively (Fig. 1A; Table 2). Among teleosts the main families represented were Lutjanidae (snappers, 7.7%), Sparidae (porgies, 6%), Hemiramphidae (halfbeaks, 4.4%), Caran-

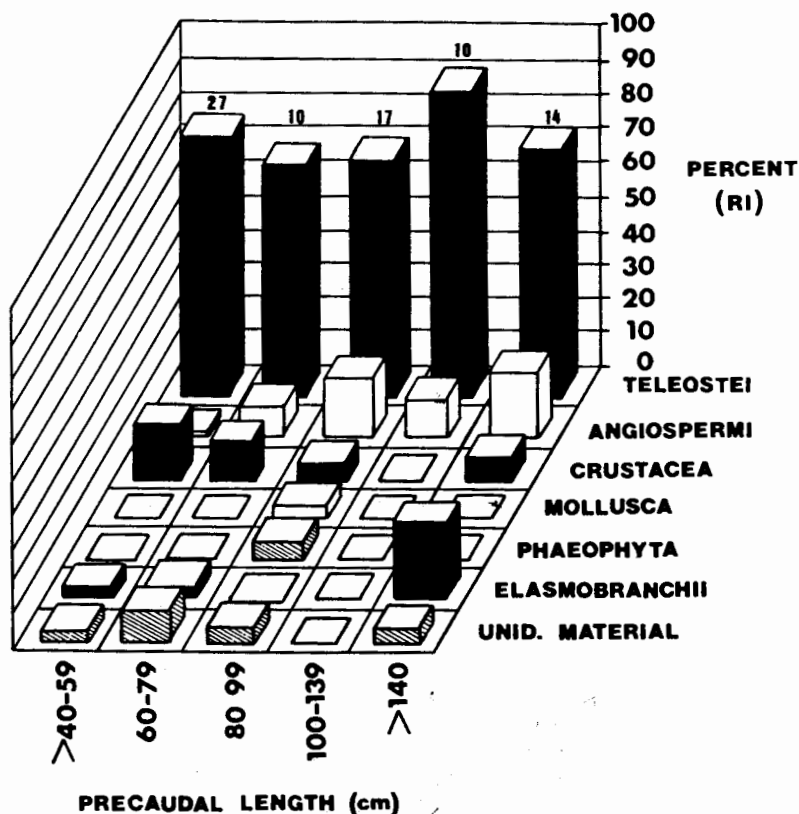


Fig. 2. Variation in the RI of the major food categories in the diet of five length classes of the lemon shark, *Negaprion brevirostris*, captured in the Florida Keys and at Bimini, Bahamas (data set 1). Sample size for each length class is given in the figure.

gidae (jacks, 4.4%), Ophichthidae (snake eels, 3.9%), and Batrachoididae (toadfish, 3.7%). Penaeid shrimps were the major component of the crustacean group, and mollusks consisted exclusively of cephalopods, *Octopus* sp. Turtle grass, *Thalassia testudinum*, represented 11% of the RI.

Because most stomachs were collected from sharks in the 40–99 cm size range, with about half of the sharks captured in the summer, we could not adequately compare the diet of the shark among size classes or among seasons. However, the data available suggested that elasmobranchs were more important in the diet of the largest size class (>140 cm PCL [$\chi^2 = 58.5$, $P \leq 0.01$]; Fig. 2). Mollusks appeared only in the 80–99 cm PCL class, whereas crustaceans were not found in the 100–139 cm PCL class, probably due to small sample size.

Data set 2: Of the 86 stomachs examined, a total of 64 contained food. The major prey group was teleosts, on a per number (75.4%),

frequency (131.2%), and dry weight (98.4%) basis (Table 3), whereas mollusks and crustaceans were considerably less important amounting to 1.5% N, 3.1% F, 0.9% W, and 7.7% N, 14.1% F, 0.4% W, respectively. The RI showed that teleosts comprised almost 80% of the diet, whereas mollusks and crustaceans represented only 1.5% and 5.8%, respectively (Fig. 1B; Table 3). The most important families of bony fishes represented were Sparidae (20%), Gerreidae (mojarra, 10%), Lutjanidae (8.5%), Cyprinodontidae (killifishes, 8.5%), Haemulidae (grunts, 5%), Sphyraenidae (barracuda, 4%), and Atherinidae (silversides, 4%) (Table 3). The pink shrimp, *Penaeus duorarum*, was less important (0.86%) than the blue crab, *Callinectes* sp. (4.9%), in the crustacean category. *Octopus* sp. was the only component in the mollusk category. Turtle grass (9.8%), manatee grass (1.82%), and other unidentified plant material (1.24%) amounted to 12.9% of the total RI.

TABLE 3. SUMMARY OF FOOD CATEGORIES IN THE DIET OF 64 YOUNG LEMON SHARKS, *Negaprion brevirostris*, FROM THE FLORIDA KEYS (DATA SET 2), EXPRESSED AS PERCENT BY NUMBER (%N), FREQUENCY OF OCCURRENCE (%F), AND PERCENT WEIGHT (%W). Also shown is the RI, which is calculated for each food type as the sum of %N, %F, and %W, expressed as a percentage of the total %N, %F and %W for all food types.

Food item	%N		%F		%W		RI
	n	%	F	%	wt (g)	%	
Pisces	98	75.4	84	131.2	317.0	98.4	79.8
Teleostei							
Atherinidae	7	5.3	6	9.4	1.3	0.4	3.9
Batrachoididae	3	2.3	3	4.7	13.0	4.0	2.8
Belonidae	2	1.5	2	3.1	1.4	0.4	1.3
Cyprinodontidae	16	12.2	12	18.7	4.6	1.4	8.4
Ephippidae	1	0.7	1	1.5	0.1	0.0	0.3
Gerreidae	13	10.0	11	17.2	32.1	9.9	9.7
Gobiidae	1	0.7	1	1.5	0.3	0.1	0.6
Haemulidae	3	2.3	3	4.7	40.6	12.6	5.1
Lutjanidae	8	6.1	7	10.9	62.8	19.5	8.5
Mugilidae	1	0.7	1	1.5	2.0	0.6	0.9
Scaridae	1	0.7	1	1.5	0.8	0.3	0.7
Sparidae	18	13.7	16	25.0	119.0	36.9	19.8
Sphyraenidae	2	1.5	2	3.1	30.4	9.4	3.7
Unid. teleosts	22	16.8	18	28.2	8.5	2.6	12.4
Mollusca	2	1.5	2	3.1	2.9	0.9	1.4
Crustacea	10	7.7	9	14.1	1.4	0.4	5.8
Angiospermi	21	16.1	21	32.8	0.8	0.3	12.9

Food consumption.—Empty stomachs, number of items per stomach, and stages of digestion: a total of 22 empty stomachs (25.6%) was found. A Chi-square test revealed no significant differences in the proportion of empty stomachs among eight 3 h time intervals ($\chi^2 = 1.032$, $P > 0.05$). The proportion of empty stomachs in males and females was not independent of time of day (G-test [$G = 6.2$ with Yate's correction, $P \leq 0.05$], Sokal and Rohlf, 1981). The proportion of empty stomachs (both sexes combined) appeared to be higher during daytime. However, an a posteriori test for the equality of two percentages revealed that this difference was not statistically significant ($t = 1.9$, $P > 0.05$, $n = 86$).

Of the 64 stomachs containing food, 36 (56.2%) contained a single food item, whereas multiple food items were found in the other 28 (43.8%) stomachs. Of the 36 stomachs containing only one food item, 21 (32.8% of the total 64 sharks) were in a late stage of digestion (stages 5–7). The distribution of qualitative stages of digestion assigned to each food item showed that items appeared in all stages of digestion. Differences between stage-of-digestion values

of first and last food items were calculated for 24 stomachs containing multiple food items and a mean difference of 2.25 (± 1.67 SD) stage-of-digestion units, equivalent to a feeding duration of approx. 11 h was found.

Calorimetry and stomach capacity.—Energy value, water, and ash content of the most representative prey items in the diet of young lemon sharks from the Florida Keys are listed in Table 4. A mean energy value of 4.6 kJ/g live weight was obtained for food consumed by sharks from data set 2. Mean maximum capacity of the stomachs was 5.7% (± 2.6 SD) BW (assuming the density of fish prey is 1 g/cc; Jones and Geen, 1977). Excluding empty stomachs, the mean quantity of food in the stomach of sharks from data set 2 (0.55% BW) was 9% of maximum capacity.

Weight of stomach contents, feeding periodicity, and tidal effects.—Weight of stomach contents (g dry weight/kg shark) of males and females was not significantly different (Mann-Whitney U-test, $t = 0.765$, $P > 0.05$, $n = 86$). To test for the

TABLE 4. DATA COLLECTED DURING CALORIC ANALYSIS OF FOOD ITEMS IN THE DIET OF YOUNG LEMON SHARKS, *Negaprion brevirostris*, FROM DATA SET 2.

Species	%Water	Dry/live wt%	%Ash	kcal/g dry wt	kcal/g ash-free dry wt	kcal/g live wt	kJ/g dry wt
<i>Octopus</i> sp.	85.9	14.1	1.75	4.813	4.897	0.679	20.137
<i>Penaeus duorarum</i>	88.1	18.9	9.18	4.371	4.772	0.826	18.288
<i>Callinectes</i> spp. ^a	67.4	32.6	46.40	3.202	5.974	1.044	13.397
<i>Strongylura marina</i>	65.8	34.2	12.49	—	—	—	—
<i>Membras martinica</i>	66.1	33.9	26.68	3.386	4.289	1.148	14.167
<i>Floridichthys carpio</i>	73.4	26.6	18.13	3.941	4.655	1.048	16.489
<i>Gerres cinereus</i>	73.9	26.1	19.60	3.837	4.589	1.001	16.054
<i>Eucinostomus</i> sp.	74.1	25.9	11.76	4.544	5.078	1.177	19.012
<i>Sphyræna barracuda</i>	69.7	30.3	9.57	4.404	4.825	1.334	18.426
<i>Archosargus rhomboidalis</i>	70.1	29.9	9.49	4.482	4.907	1.340	18.753
<i>Lutjanus</i> sp.	64.4	35.6	7.40	4.660	5.005	1.659	19.497
<i>Haemulon</i> sp.	60.6	39.4	4.61	4.729	4.947	1.863	19.786
<i>Opsanus beta</i> ^b	77.9	22.1	18.24	4.328	5.294	0.957	18.120

^a From Thayer et al. (1973).^b From M. Cummings (pers. comm.).

existence of feeding periodicity, the weights of stomach contents for each of the eight 3 h time intervals were subjected to a Kruskal-Wallis test (adjusted $H = 8.55$, $P > 0.05$, $n = 86$) which failed to reveal any discontinuity in diel feeding activity (Fig. 3A). To determine whether this finding was an artifact due to the length of the time interval chosen, the data were further rearranged into six 4 h time intervals (Fig. 3B, solid line), resubjected to a Kruskal-Wallis test (adjusted $H = 6.93$, $P > 0.05$, $n = 86$), and again no discontinuity was detected. An addi-

tional set of six 4 h time intervals (Fig. 3B, broken line) was resubjected to the Kruskal-Wallis test (adjusted $H = 4.51$, $P > 0.05$, $n = 86$) again revealing no discontinuity. A high variability was apparent at all sampling times. The amount of food in the stomach of males and females caught during the day and night was not significantly different (two-way ANOVA with log-transformed data). Likewise, flood and ebb tides did not appear to have an effect on the weight of stomach contents of males and females (two-way ANOVA with log-transformed data).

TABLE 5. ESTIMATES OF DAILY RATION (PERCENT LIVE BODY WEIGHT [%BW]) FOR YOUNG LEMON SHARKS, *Negaprion brevirostris*, FROM DATA SET 2. Included are the relevant equations. For details, see text.

Method	Equation for estimating daily ration ^a	Daily ration Sample 2 (n = 86, 31.8 C)
Elliott and Persson (1978)	$C_t = \frac{(S_t - S_0 e^{-Rt})}{1 - e^{-Rt}}$; $DR = \sum C_t = \bar{W}R$	2.16
Diana (1979)	$F = \frac{B}{1 - E}$; $DR = \frac{S_0}{F}$	1.85
Olson and Mullen (1986)	$r = \frac{\bar{W}}{\int_0^\infty f(t)dt}$	1.56
Laboratory 1 (L-1)	$DR = \frac{G}{K_1}$	1.66
Laboratory 2 (L-2)	$DR = 1.25(G + M)$	1.88

^a C_t : consumption between sampling periods; S_t : amount of food in stomach at the end of the interval between catches; S_0 : amount of food in stomach at the beginning of the interval between catches; R : exponential rate of gastric evacuation; DR : daily ration; \bar{W} : mean weight of food in stomach; F : feeding frequency; B : time for complete gastric evacuation; E : proportion of empty stomach; S_0 : initial meal size; $f(t)$: proportion of food remaining in stomach; G : growth; K_1 : gross conversion efficiency; M : laboratory-derived metabolic rate.

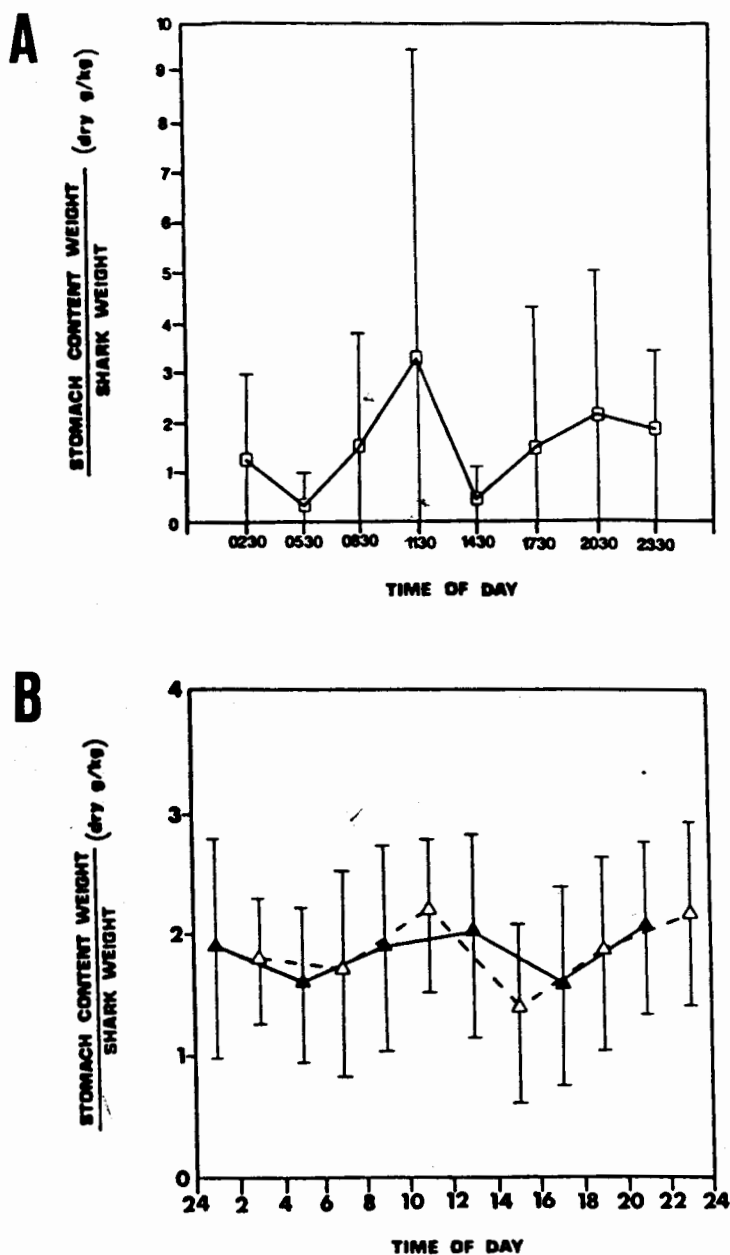


Fig. 3. Diel variation in mean ratio of dry weight of stomach contents to wet weight of shark (g/kg) for 86 young lemon sharks, *Negaprion brevirostris*, from data set 2. Each value represents the mid-point of a given time interval. Vertical lines designate ± 1 SD: A) open squares are the means for each of eight 3 h time intervals, starting at 0100 h; B) solid triangles are the means for each of six 4 h time intervals, starting at 2300 h; open triangles are the means for each of six 4 h time intervals, starting at 0100 h.

Estimates of daily ration.—The estimates of daily ration obtained by the different methods are listed in Table 5. The Elliott and Persson model produced a value of 2.16% BW and also allowed

us to investigate the diurnal feeding cycle of the young lemon shark (Table 6).

In the Diana model, meal frequency (F) was 32.9 h (24.5/1–0.256) or 1.37 d for the expo-

TABLE 6. DIET FEEDING CYCLE AND TOTAL DAILY RATION (PERCENT LIVE BODY WEIGHT [%BW]) FOR YOUNG LEMON SHARKS, *Negaprion brevirostris*, FROM DATA SET 2 BY THE ELLIOTT AND PERSSON METHOD (1978). Column (1) contains the eight 3 h sampling intervals during which *n* (column (3)) stomachs were sampled; time (column (2)) is the mid-point of each 3 h sampling interval.

Sampling interval (1)	Time (2)	Sample size No. 2 (n = 86) (3)	Estimates of daily ration (%BW) No. 2
0100-0400	0230	3	-0.223
0400-0700	0530	14	+0.532
0700-1000	0830	10	+1.073
1000-1300	1130	9	-0.619
1300-1600	1430	8	+0.454
1600-1900	1730	17	+0.588
1900-2200	2030	17	+0.166
2200-0100	2330	8	+0.191
0100-0400	0230	3	—
Overall		86	2.16

nential model, and 47 h (35/1-0.256) or 1.96 d for the linear model. Mean reconstructed meal size (S_0) for smaller prey items digested in an exponential manner was 0.66% BW (± 0.54 SD) and 2.68% BW (± 3.03 SD) for the larger items digested in a linear manner. Thus, daily ration becomes 0.48% BW (0.66/1.37) and 1.367% BW (2.68/1.96) respectively, yielding a total daily ration of 1.85% BW.

In the Olson and Mullen model \bar{W} was 1.6 g (± 3.1 SD) for small food items, and 21.4 g (± 29.7 SD) for larger prey items. Substituting these values in equations (10) and (11), respectively, yields a feeding rate of 0.284 and 1.287. Total daily ration then becomes 1.56% BW (0.28 + 1.28).

For the first of the laboratory methods (L-1), when the estimate of growth from the field (3.8 g/d) is plotted in the ration-production relation determined in the laboratory, it yields a daily ration of 32.1 g/d or 1.66% BW for an average weight shark in the middle of its first year of life. For the other laboratory method (L-2), the estimate of field growth (G) converted into joules is 20.5 kJ/d. Average metabolic rate (M) for the average size shark from data set 2 (2.42 kg) is 164 kJ/d (67.8×2.42). When the values of G and M are substituted in the energy budget equation, the energy value for food consumed becomes 230.6 kJ/d. The daily ration obtained is 45.7 g/d (230.6/5.05) or 1.88% BW.

DISCUSSION

Diet and food habits.—Our results generally agree with the fragmentary literature reports on the diet of the lemon shark. Clark and von Schmidt (1965) found that an unreported number of lemon sharks in the west central coast of Florida fed mainly on teleosts, including the catfishes *Bagre marinus* and *Arius felis*, mullet (*Mugil* sp.), and octopods. Dahlberg and Heard (1969) found a 238.9 cm lemon shark in waters of Georgia containing two stingrays. In comparison, in data set 1 two specimens of the yellow stingray, *Urolophus jamaicensis*, and unidentifiable elasmobranch remains were found in stomachs of lemon sharks. The southern stingray, *Dasyatis americana*, has also been found in the stomachs of pre-adult and adult lemon sharks and stingray spines are often found imbedded in the upper jaw cartilage of adult lemon sharks (Cortés and Gruber, pers. obs.). Snelson and Williams (1981) analyzed three stomachs of lemon sharks from the Indian River lagoon system in Melbourne, Florida, and found stingray, *Dasyatis* sp., the American eel, *Anguilla rostrata*, mullet, the striped burrfish, *Chilomycterus schoepfi*, and portunid crabs. In data set 1 snake eels (Ophichthidae) were present in 3.9% (RI) of the cases and mullets in only 1.1%. We found portunid crabs only in the smallest size group (40-59 cm PCL). Dodrill (unpubl.) found teleosts in 27% of the 13 lemon shark stomachs he analyzed, caught along Melbourne Beach, Florida. He identified the hardhead catfish, *Arius felis*, the crevalle jack, *Caranx hippos*, a balistid, and other teleosts remains. He also found an elasmobranch, a turtle flipper and a stomatopod shrimp. In comparison, in the present study jacks (Carangidae) and the hardhead catfish, *A. felis*, represented 4.4% and 1.3% of the RI, respectively.

For young lemon sharks, our findings reveal that the Florida Keys population feeds almost exclusively on teleosts. Springer (1950) reported small amphipods and other crustaceans in stomach contents of young lemon sharks, and suggested that they also feed on schools of the silver mullet, *Mugil curema*, and the striped mullet, *M. cephalus*. Schmidt (1986), working near Sandy Key in western Florida Bay near our sampling sites, found that the pink shrimp, *Penaeus duorarum*, the toadfish, *Opsanus beta*, and the pinfish, *Lagodon rhomboides*, constituted the major prey items in the diets of 18 young lemon sharks ranging in size from 57.7-99.9 cm TL.

In data set 2 of the present study, the seabream, *Archosargus rhomboidalis*, the gold-spotted killifish, *Floridichthys carpio*, snappers, *Lutjanus* sp., mojarras, *Eucinostomus* sp., grunts, *Haemulon* sp., and portunid crabs, *Callinectes* sp., were the most important food items. These results may reflect the availability of prey in each study site. Schmidt (1986) reported that the most representative food items in his diet analysis were among the most important numerically in the grass beds near his study site. Biomass studies are under way at our sampling sites to try to determine whether young lemon sharks indeed prey on the most abundant prey items, or exhibit some degree of selectivity.

Young lemon sharks appear to feed upon two main categories of fishes: small fishes that school over shallow grass beds, such as killifishes, silversides, and mojarras, which are usually swallowed whole; and larger, predatory fishes, such as young seabreams, snappers, and grunts. These larger fishes feed nocturnally on grassy bottoms and are ordinarily bitten by the sharks into pieces as attested by the presence in parts in the stomach contents. However, in one unusual case a 55.5 cm PCL lemon shark contained whole specimens of the barracuda, *Sphyraena barracuda* (22 cm), a seabream (12 cm), a mullet (24 cm), and a gold-spotted killifish (5 cm). This finding indicates that lemon sharks can be opportunistic feeders.

There appears to be an ontogenetic change in the diet of the lemon shark. As the shark ages, the variety of habitats it occupies increases. It no longer feeds on the flats exclusively but moves on to the reef, and adults can be found to at least 50 m. This ontogenetic change in both types and size of habitat brings about an increase in prey availability and prey types. For example, we found elasmobranchs and lobsters only in the stomachs of the largest sharks (>140 cm PCL), and adult jacks, ordinarily found in deeper water, consistently appeared in sharks larger than 80 cm PCL only. However, we believe that the existence of turtle grass in the diet of all the size classes studied attests to the benthic feeding habits of lemon sharks.

Diel changes in stomach contents.—The finding of food in all stages of digestion in stomachs of young lemon sharks sampled at hourly intervals indicates that there is no preferred time of the day or night when a majority of sharks feed (i.e., feeding is asynchronous in the population). The

time young lemon sharks actively feed (feeding duration) was estimated to be approximately 11 h. Medved et al. (1988) found that the feeding duration of young sandbar sharks, *Carcharhinus plumbeus*, in Chincoteague Bay, Virginia, was short relative to time for complete gastric evacuation. However, these authors found a time of 81.5 h for complete gastric evacuation of a meal, compared to the 24–41 h estimates derived from the studies of the lemon shark. We found that the duration of feeding represents $\frac{1}{3}$ of gastric evacuation time, compared to $\frac{1}{10}$ in the study by Medved et al.

We also found that of all the stomachs containing food, 50 (78%) contained only one or two food items. Any shark feeding continuously would be expected to have many food items at various stages of digestion in the stomach. However, we found only 14 (22%) stomachs containing three or more food items. Therefore, we can reasonably conclude that feeding is not continuous, but rather intermittent.

Holden (1966) and Jones and Geen (1977) reported that the spiny dogfish, *Squalus acanthias*, ceased to feed until digestion was complete. Medved et al. (1988) also suggested that young sandbar sharks cease feeding after consumption of a meal. Our data cannot clearly resolve whether young lemon sharks cease feeding after consuming a meal and wait until digestion is complete to take a new meal. On the one hand, 25% of the population had empty stomachs. Since gastric evacuation is complete in about 1–2 d, the sharks with empty stomachs had not consumed any food for at least this amount of time. In addition, 25 stomachs (representing 29% of the population) contained a single food item in a late stage of digestion ($\bar{x} = 5.5 \pm 1.0$ SD), indicating that these sharks had not consumed any food for about 28 h prior to when they were caught. These two pieces of evidence suggest that the interval between meals is at least close to digestion time in over 50% of the cases. Furthermore, feeding frequency estimated by the Diana model ranged from 33–47 h. Therefore, these three pieces of evidence (i.e., percentage of empty stomachs, occurrence of a single food item in a late stage of digestion, and feeding frequency) lend support to the hypothesis that lemon sharks cease feeding after consuming a meal and do not feed again until digestion is complete or almost complete. On the other hand, we found seven stomachs with food items having differences between stage-of-digestion values ranging from 3–6 units, indi-

cating that feeding does not always cease after consumption of a meal, or that a meal may consist of several short feeding bouts separated in time and consisting in turn of different prey with different digestibilities. Laboratory observations showing that sharks will take an additional meal with food still in the stomach further support this interpretation.

Lemon sharks in the laboratory increase activity and metabolic rate at the onset of darkness (Gruber, 1984), probably as a result of an internal rhythm. Longval et al. (1982) found a 4 d cycle in food intake of captive lemon sharks and speculated that the peak may have been mediated by an internal rhythm. Finally, Gruber (1984) obtained preliminary telemetry data showing that lemon sharks are more active at night. We found no temporal difference in the amount of food in stomachs of lemon sharks. The high variability present at all sampling times seems to indicate that young lemon sharks do not feed preferentially at any time of the day or night. However, our study is continuing and a larger sample size will allow us to reveal any increased nocturnal feeding activity as a consequence of the suggested internal rhythms, and whether feeding activity is influenced by the tidal cycle. In the present study tidal cycle was not found to affect feeding activity.

To summarize, it appears that a majority of young lemon sharks would actively feed for about 11 h, regardless of time of the day or tidal phase, then go without feeding for the next 33–47 h.

Daily ration.—Our estimates of daily ration varied between 1.56% BW and 2.16% BW at a mean temperature of 31.8 C. The assumption of continuous feeding implicit in the Elliott and Persson model is not valid for the lemon shark. However, the violation of this assumption does not affect the estimate of daily ration because the interval between samples was kept to 3 h or less. Similarly, evacuation of large, nutrient-rich prey items does not seem to follow an exponential function, but a linear pattern (Jobling, 1987). Large food items were found in a number of cases in the stomachs of lemon sharks, suggesting that the assumption of an exponential evacuation rate was violated and that the Elliott and Persson model was not totally adequate to estimate daily ration.

The assumptions implicit in the Diana model were generally well satisfied. Thus, we have shown that feeding is asynchronous and inter-

mittent, and feeding bouts are relatively short. Time between meals, however, is not always longer than digestion time. Estimating daily ration separately for small, easily digested prey and for larger food items seems appropriate in the light of the evidence (Jobling, 1987) existing on the pattern of gastric emptying in fish.

The estimate of daily ration by the Olson and Mullen model was 1.56% BW. This method has the advantage of not making any assumptions about the pattern of food evacuation. Estimating a separate feeding rate for each of the two prey categories considered (small and large) in the present study seems therefore adequate.

Multiple meals may have biased the daily ration estimates by both the Elliott and Persson, and the Olson and Mullen models, since these methods assume that every food item is evacuated independently of other food items in the stomach, an assumption that Persson (1984) found to be unsatisfied in his study of daily ration in the European perch, *Perca fluviatilis*.

The adequateness of the laboratory methods (L-1 and L-2) is associated with the reliability of the estimates of growth and metabolism. It is particularly difficult to assess how well the value of metabolic rate derived from the laboratory studies fits the real energy expenditure in the wild. This is because it is hard to evaluate the magnitude and direction of the overall change in metabolism in the field. Whereas in the laboratory the sharks were held at a constant temperature of 25 C, in the wild sharks experienced a range of temperatures around 31.8 C. Furthermore, the energy costs of searching and foraging are unknown. One of us (SG) is presently addressing these questions by measuring heart-rate and using ultrasonic telemetry to determine activity and metabolism in free-ranging lemon sharks.

Although none of the models tested is completely ideal for estimating the daily ration of the lemon shark, the assumptions implicit in some of them are relatively well satisfied. Furthermore, our estimates of daily food consumption of the young lemon shark obtained through the five methods are in a narrow range, suggesting that they are close to the actual value of daily ration.

A value between 1.5% BW and 2.1% BW indicates that the daily ration of young lemon sharks is in the lower end of the range of daily rations of teleosts (Table 7). This is probably because, as a literature review indicated, most teleosts have a gastric evacuation time about 2.5

TABLE 7. DAILY RATION (DR) AND TOTAL GASTRIC EVACUATION TIME (TGET) FOR SEVERAL ELASMOBRANCH AND TELEOST SPECIES.

Species	DR	TGET (h)	Evacuation model	Study
Elasmobranchs				
<i>Squalus acanthias</i> (spiny dogfish)	1.3 (10 C)	124	Linear	Jones and Geen (1977)
<i>Isurus oxyrinchus</i> (shortfin mako)	3.1 (19 C)	?	?	Stillwell and Kohler (1982)
<i>Carcharhinus plumbeus</i> (sandbar shark)	1.0 (25 C)	71–92 (22–30 C)	Gompertz	Medved et al. (1988)
<i>Negaprion brevirostris</i> (lemon shark)	1.5–2 (23–32 C)	25–41 (20–29 C)	Exponential, linear	Schurdak and Gruber (1989)
Teleosts				
<i>Thunnus albacares</i> (yellowfin tuna)	2.8–4.5	9	Linear	Olson and Mullen (1986)
<i>Stizostedion vitreum</i> (walleye)	1–3	12	Linear	Swenson and Smith (1973)
<i>Micropterus salmoides</i> (largemouth bass)	5.5–8.4 (24–25 C)	14–19 (22–25 C)	Linear	Molnar and Tolg (1962); Hunt (1960)

times shorter than the lemon shark at the same temperature ranges. Thus, faster evacuation rates probably enhance food intake and growth in teleosts. To date, only three studies have provided estimates of daily ration in other elasmobranchs (Table 7). Jones and Geen (1977) reported an average value of 1.3% BW at 10 C for captive spiny dogfish, a value consistent with the slow growth rate, low metabolic rate, and long evacuation time of this species. Daily ration of the shortfin mako, *Isurus oxyrinchus*, was estimated at around 3.2% BW at 18.8 C (Stillwell and Kohler, 1982). Lamnid sharks and other fast-swimming, active teleosts like tuna, *Thunnus* sp., and billfishes (Istiophoridae) are predators capable of maintaining viscera and muscle temperatures several degrees above ambient water temperature (Carey and Teal, 1969). This capacity to retain metabolic heat probably speeds up digestive processes, shortens the time for gastric emptying and enhances food intake. A similar mechanism could operate in the great white shark, *Carcharodon carcharias*, which appears to keep elevated intragastric temperatures (McCosker, 1987). Finally, Medved et al. (1988) estimated the daily ration of young sandbar sharks at around 1% BW at 25 C. The difference in the daily ration estimates for young lemon sharks and sandbar sharks is probably due to a slightly faster growth rate of the lemon shark (Henningsen and Gruber, unpubl.), lower metabolic rate and energy requirements of the sandbar shark (not reported), ambient water

temperature in both studies, and energy value of food consumed by both species.

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